View metadata, citation and similar papers at core.ac.uk

brought to you by CORE

provided by Elsevier - Publisher Connector

Available online at www.sciencedirect.com

ScienceDirect

South African Journal of Botany 74 (2008) 647–650

SOUTH AFRICAN JOURNAL OF BOTANY

www.elsevier.com/locate/sajb

Stem anatomy of *Acanthosicyos horridus* (Cucurbitaceae)

B. Kartusch[a,*], R. Kartusch[b]

[a] *Department for Integrative Biology und Biodiversity Research (DIB), Botanical Institute, University of Natural Resources and Applied Life Sciences, Vienna, Gregor Mendel Str. 33, A-1180 Vienna, Austria*

[b] *Department for Ecophysiology and Functional Anatomy of Plants, University of Vienna, Althanstr. 14, A-1090 Vienna, Austria*

Received 8 November 2007; received in revised form 18 March 2008; accepted 1 April 2008

Abstract

The leafless, green stemmed, non-succulent plant *Acanthosicyos horridus* (Cucurbitaceae) is an endemic species of the foggy Namib Desert. The transverse stem section shows 15 white ridges alternately with 15 green furrows. The complete cylinder of extraxylary fibres in the primary cortex is typical of the cucumber family. Fifteen bicollateral vascular bundles each are situated in an inner and an outer circle. Secondary growth is typical for the vine type. Articulated ramified sap filled idioblasts are a special feature not described until now in *A. horridus*.
© 2008 SAAB. Published by Elsevier B.V. All rights reserved.

Keywords: *Acanthosicyos*; Stem anatomy; Idioblasts

1. Introduction

Acanthosicyos horridus (Cucurbitaceae; indigenous name ! Nara) is a leafless non-succulent C_3-plant with a green stem. It grows only in the Namib Desert around Walvis Bay in Namibia (Engler and Prantl, 1891; Van Den Eynden et al., 1992). The melon-like fruits of the !Nara plants are the main staple of the local Topnaar people (Henschel et al., 2004) and the roots are of importance for the pharmaceutical industry, since several different cucurbitaceous substances are extracted, and which for example are used to induce tumour necrosis (Hegnauer, 1964).

The costal foggy Namib Desert is one of the warm deserts of the world. Fog deserts rarely receive measurable rainfall, but precipitation from condensing fog may exceed 150 mm per year (Gibson, 1996). Desert plants employ a number of different strategies to deal with environmental stresses, which are mainly drought, heat, and high irradiation.

2. Materials and methods

The material used for the investigation was collected in the Kuiseb river valley near the desert research station at Gobabeb (23° 33.704 S latitude, 15° 02.466 E longitude) on habitats located near the southern bank of the Kuiseb river. Two 15-cm long twigs from aboveground and one 5-cm long piece of a stem from under a sand hummock were collected, dissected in approximately 3-cm long pieces, and then fixed immediately in an ethanol and water mixture (1:1). A sledge microtome (Reichert, Vienna) was used to prepare transverse and longitudinal sections approximately 35–45 μm thick. The sections were stained in picric acid (saturated solution) and acid fuchsin (1%), both dissolved in distilled water, or in safranin (1 g/100 ml a.d.) and astra blue (0.5 g astra blue and 2 g tartaric acid/100 ml a.d.). Specimens were viewed using a CH3-microscope (Olympus) and images captured using a Camedia C-4040 ZOOM (Olympus).

3. Results

3.1. Functional morphology

The stems of *A. horridus* can grow to many meters long with the greater part covered by sand which collects around the plant.

* Corresponding author. Tel.: +43 1 47654 3191.
E-mail address: birgit.kartusch@boku.ac.at (B. Kartusch).

0254-6299/$ - see front matter © 2008 SAAB. Published by Elsevier B.V. All rights reserved.
doi:10.1016/j.sajb.2008.04.001

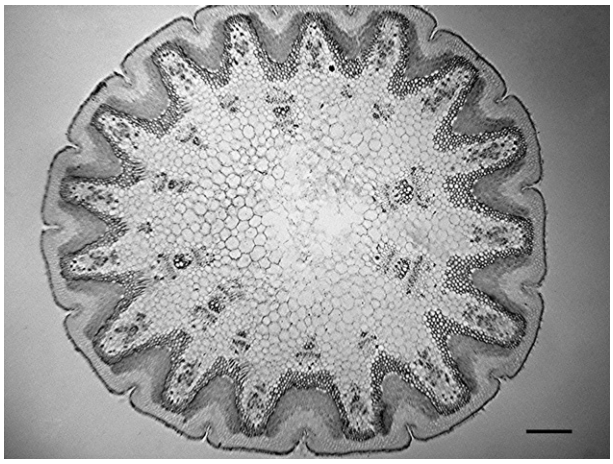

Fig. 1. Transverse section of a stem of *A. horridus*. Bar 100 µm.

Spines are only found on plant material on the top of such hummocks. These rigid thorns are metamorphosed branches arranged helically (Gibson 1996). The roots may be up to 100 m long (Kutschera et al., 1997) and collect water from subterranean river beds; in this region mainly from the Kuiseb river.

3.2. Structure of the primary stem

3.2.1. Transverse section

Since leaves are absent, the photosynthetically active tissue is located in the stems. The stems have deep longitudinal furrows and ridges. The chlorenchyma is concentrated around the furrows, while strands of collenchyma are localized on the ridges. In a transverse section of a primary stem, 15 white ridges alternate with 15 green furrows (Fig. 1). The cone shaped epidermis cells are situated towards the outside of both the furrows and the ridges. A multiple epidermis develops only in the furrows, varying in thickness from 2 to 6 layers of cells. The outermost layer resembles the ordinary epidermis in that it has a rather 4.5–5 µm thick cutinized outer cell wall covered by a 1.5–2 µm thick cuticle. The cutinized cell wall fills the gaps which are formed by the cone-shaped epidermal cells.

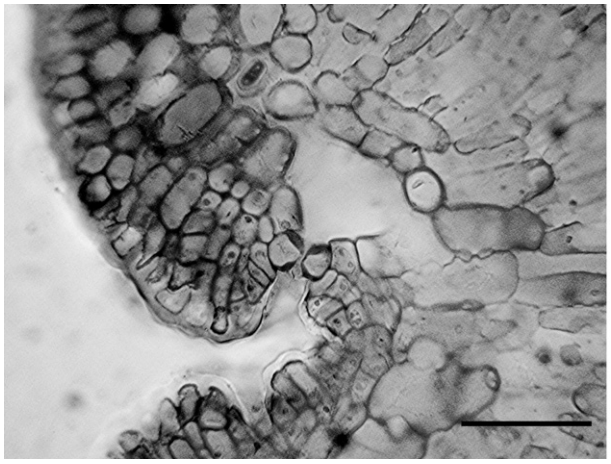

Fig. 2. Transverse section of a stem of *A. horridus*. Stomata are deeply sunken. Bar 50 µm.

Stomata are only present in the furrows. The guard cells are deeply sunken, and the stomata open into large substomatal chambers (Fig. 2). In addition to stomata, the epidermis in the grooves also has trichomes, either as single-cells, multicellular hairs or glandular hairs with multicellular heads. Angular as well as lacunar collenchyma without chloroplasts is situated below the epidermal cells of the ridges.

The furrows are bordered by small cells without intercellular spaces and chloroplasts. More deeply into the furrows, parenchyma cells without chloroplasts are found underneath the epidermis, associated with large intercellular spaces, similar to the spongy parenchyma found in leaves. Beneath these cells there are three to five layers of elongate-prismatic parenchyma cells similar to the palisade parenchyma of leaves of C_3 plants with small intercellular spaces and containing many chloroplasts. The furrows are bordered by small cells without intercellular spaces and chloroplasts are lacking.

Extraxylary fibres provide a boundary between the ridges and the furrows towards the interior of the stem. Such a cylindrical arrangement of the fibres is typical for the cucurbits. It is not circular as usual but arranged in the shape of a star in cross-section. In the ridges the fibres divide the small cells on the border of the palisade-like cells from the inner ground parenchyma of the stem. Between the epidermis of the ridge tips and the fibres about three or four layers of angular collenchyma are found.

The smaller bundles are close to the tips of the furrows, the 15 bigger ones are located inside the innermost portion of the star of extraxylary fibres, embedded in the inner ground parenchyma (Fig. 3). The presence of phloem on both sides of the xylem makes the bundle bicollateral. Like other plants with similar circles of extraxylary fibres *A. horridus* forms no fibres in the protophloem.

3.2.2. Longitudinal section

A little known feature of the cucumber family can be observed in *A. horridus*. Longitudinal sections of stems clearly show articulated anastomosing idioblasts (originally mentioned

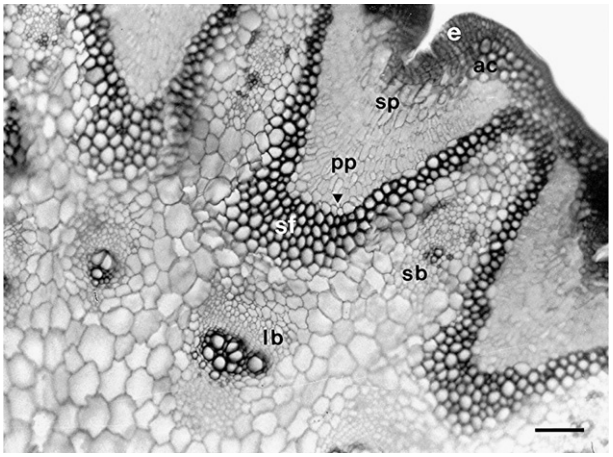

Fig. 3. Transverse section of a stem of *A. horridus*. *e* Multiple epidermis; *ac* angular collenchyma, *sp* subepidermal parenchyma composed of cells with few chloroplasts and big intercellular spaces; *pp* elongated prismatic cells with many chloroplasts; *arrowhead* one cell layer without intercellular spaces and without chloroplasts; *sf* sclerenchymatic fibers; *lb* large bundle; *sb* small bundle. Bar 100 µm.

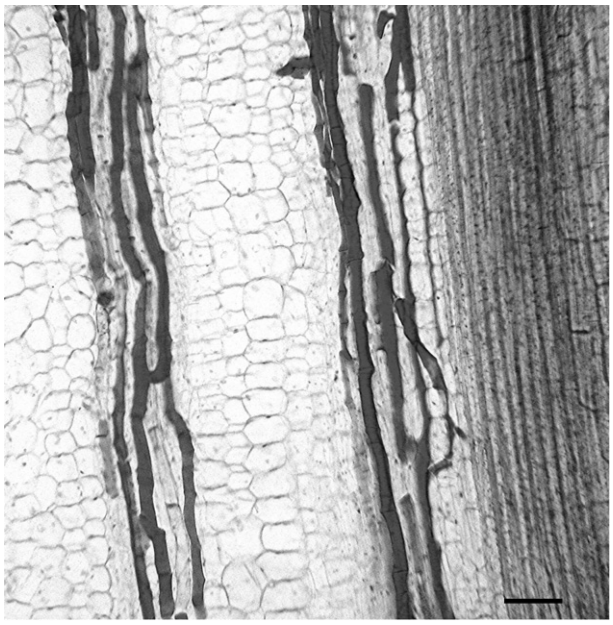

Fig. 4. Idioblasts stained with acid fuchsin-picric acid (longitudinal section). Bar 100 μm.

by Braemer, 1893), resembling laticifers, but which, because of their content, cannot be classed as laticifers (Esau, 1965). These idioblasts are stained selectively and intensively with acid fuchsin-picric acid (Fig. 4). The partition walls show primary pit fields which are rarely observed in laticifers (Fig. 5, arrows). Most of the idioblasts are observed at the periphery of the circle formed by the outer bundles and seem to be associated with strands of extrafascicular sieve tubes and companion cells. In

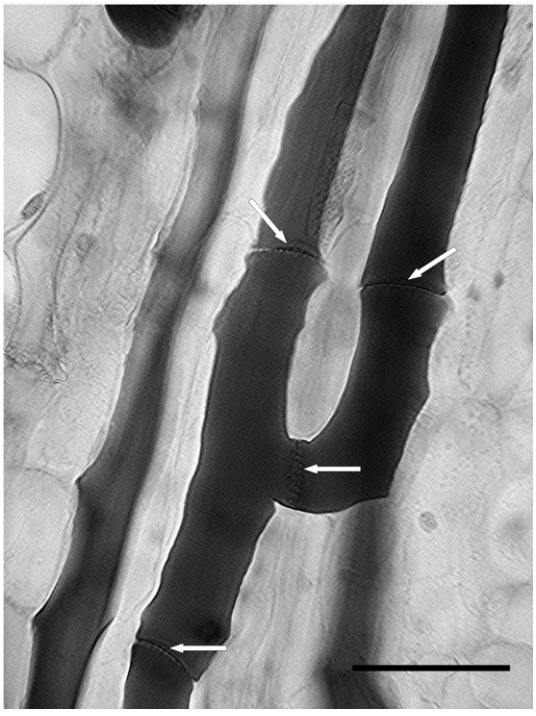

Fig. 5. Primary pit fields on the partition walls between idioblast cells (arrows). Longitudinal section. Bar 50 μm.

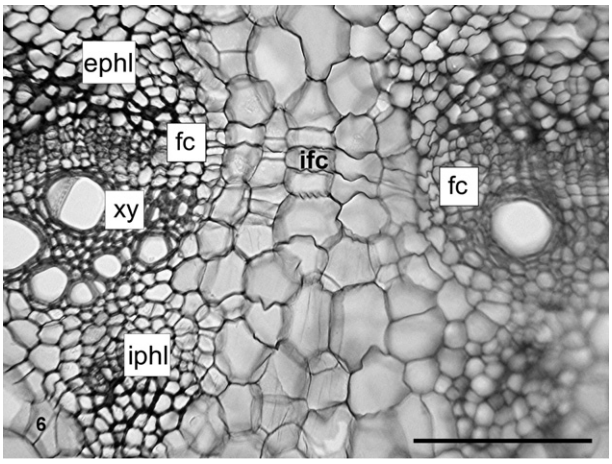

Fig. 6. Beginning of secondary growth in a stem of *A. horridus*. Transverse section. *ifc* interfascicular cambium; *fc* fascicular cambium; *inphl* internal phloem; *exphl* external phloem; *xy* xylem. Bar 100 μm.

the intact plant these idioblasts are turgid and in water-potential equilibrium with the surrounding parenchyma cells. When the idioblast system is cut open, a pressure gradient is established and flow occurs towards the cut where the turgor pressure has been reduced to zero. This fact explains why liquid droplets appear on the surface of a cut stem of *A. horridus*. This water is not normally released from the xylem vessels because of their highly negative water potential.

3.2.3. Secondary growth of the stem

Secondary growth of the stem of *A. horridus* can only be observed in those parts of the stem which are buried in the moist sand of the hummocks and only in the bigger bundles. Commonly the cambium arises in the form of a cylinder between the primary xylem and the primary phloem (Fig. 6). In bicollateral vascular bundles with vascular cambium on both sides of the xylem the cambium only arises between the xylem and the outer phloem while the inner cambium has lost its function and does not produce secondary vascular tissue. The outer cambium remains in the same relative position and produces secondary xylem towards the inside of the axis and secondary phloem to the outside. The primary vascular tissues of *Acanthosicyos* form a system of strands. The interfascicular cambium only produces ray parenchyma, and therefore, the secondary vascular tissue also appear as strands that are typical of the vine type of secondary growth (Esau, 1965, 1977).

4. Discussion

A. horridus is the only member of the Cucurbitaceae which is adapted to survive the extreme climate of the Namib desert (Hebeler, 2000). The obvious difference between *A. horridus* and other members from the cucumber family is the absence of leaves. This is a characteristic survival strategy which occurs in all warm deserts (Ehleringer, 1985; Gibson, 1996; Smith and Nobel, 1986).

The green stem of *A. horridus* is well adapted to the harsh environmental conditions of the Namib desert in a number of

different ways. Of the anatomical parameters, the multiserate epidermis reduces transpiration and functions as a radiation filter reflecting UV, some PHAR, and IR. The stomata are deeply sunken in the furrows. The thickly cutinized epidermis cells are an extremely important adaptation for protecting the long-lived chlorenchyma of the stems from UV-damage (Gibson, 1996).

A. horridus is one example of the aphyllous phanerophytes occurring in all warm deserts; its green stem tissue functions like the leaf palisade parenchyma of C_3-species. These palisade-like cells are situated on both borders of the furrows. The gas exchange is therefore reduced (Hebeler, 2000; Hebeler et al., 2004) and a supplementary protection against high irradiation must be present. For a stem in an upright position the amount of the absorbed light will be minimal during the hours with the strongest irradiance (Von Willert et al., 1992). A certain part of the incoming light is to be reflected, as indicated by the silvery pale-green appearance of the plant.

Another mechanism of adaptation to the harsh environmental conditions is the formation of hummocks. The greater part of the plant is buried in the moist sand of the hummocks, where no assimilation occurs. The chloroplasts of the palisade-like cells retrogress into leucoplasts. Thus only a small part of the plant is able to assimilate, and transpiration is presumably absent from the buried parts. Many stem-borne adventitious roots in the hummocks indicate that water is taken up from precipitated fog (Kutschera et al. 1997).

The presence of a ramified system of idioblasts might be of importance. The idioblasts of *A. horridus* are a series of fused cells filled with an aqueous solution containing among others a high concentration of cucurbitacines typical for Cucurbitaceae (Braemer, 1893, cited in Hegnauer, 1964). Solereder (1899) as well as Metcalf and Chalk (1950) have pointed to the lack of internal secretory structures in the cucumber family, but Braemer (1893) and Cortesi (1960) observed simply or compound idioblasts in *Bryonia*, *Citrullus* and *Ecballium*. In *A. horridus*, the idioblasts are stained selectively and intensively with acid fuchsin-picric acid, thereby showing a primary nature of their cell walls (Bruni and Tosi, 1980). These solution-filled idioblasts may act as a water-storage compartment, thus balancing the water management. Therefore we conclude that the main stress factor in the case of *A. horridus* is high irradiation, and that its anatomical and physiological adaptations have developed in relation to this stress.

Acknowledgements

Dr. Joh Henschel, DRFN & TCF, Gobabeb Training and Research Centre, Gobabeb, Namibia, and his staff are thanked for their hospitality and technical support.

References

Braemer, L., 1893. De la localisation des principes actifs des Cucurbitacées. Thèse Doct. (Med.) Univ. Toulouse.

Bruni, A., Tosi, B., 1980. A method for localizing embryonal laticifers by combined conventional and fluorescence microscopy. Protoplasma 102, 343–347.

Cortesi, R., 1960. Inventaire anatomique des végétaux supérieurs: (spermatophytes et quelques ptéridophytes). Institute de Botanique Générale, Université de Genève.

Ehleringer, J., 1985. Annuals and perennials of warm deserts. In: Chabot, B.F., Mooney, H.A. (Eds.), Physiological Ecology of North American Plant Communities. Chapman and Hall, New York, pp. 162–180.

Engler, A., Prantl, K., 1891. Die natürlichen Pflanzenfamilien. IV. Teil, 5. Abt. Wilhelm Engelmann, Leipzig, pp. 22–24.

Esau, K., 1965. Plant Anatomy, 2nd ed. John Wiley & Sons, Inc., New York, London, Sidney.

Esau, K., 1977. Anatomy of Seed Plants, 2nd ed. John Wiley and Sons, New York, Santa Barbara, London, Sidney, Toronto.

Gibson, A.C., 1996. Structure–function Relation of Warm Desert Plants. Springer Verlag, Berlin.

Hebeler, F., 2000. Structural and ecophysiological shoot features of the leafless cucurbit *Acanthosicyos horridus*, a keystone endemic of the Namib desert. Diploma Thesis, Justus-Liebig-Universität Giessen.

Hebeler, F., Botha, C.E.J., Van Bel, A.J.E., 2004. Water, photosynthesis and transpiration of !Nara /*Acanthosicyos horridus*. In: Henschel, J., Dausab, R., Moser, P., Pullett, J. (Eds.), !Nara. Fruit for the Development of the Kuiseb Topnaar. Namibian Scientific Society, Windhoek, Namibia.

Hegnauer, R., 1964. Chemotaxonomie der Pflanzen. Bd. III. Birkhäuser, Basel, Stuttgart, pp. 608–676.

Henschel, J., Dausab, R., Moser, P., Pullett, J., 2004. !Nara. Fruit for Development of the !Kuiseb Topnaar. Namibia Scientific Society, Windhoek, Namibia.

Kutschera, L., Lichtenegger, E., Sobotik, M., Haas, D., 1997. Die Wurzel, das neue Organ. Eigenverlag. Pflanzensoziologisches Institut, Klagenfurt.

Metcalf, C.R., Chalk, L., 1950. Anatomy of the Dicotyledons. Clarendon Press, Oxford.

Smith, S.D., Nobel, P.S., 1986. Deserts. In: Baker, N.R., Long, S.P. (Eds.), Photosynthesis in Contrasting Environments. Elsevier, Amsterdam, pp. 13–62.

Solereder, H., 1899. Systematische Anatomie der Dicotyledonen. Ferdinand Enke, Stuttgart, pp. 439–448.

Van Den Eynden, V., Vernemmen, P., Van Damme, P., 1992. The Ethnobotany of the Topnaar. University of Gent. The Commission of European Community.

Von Willert, D.J., Ellert, B.M., Werger, M.J.A., Brinkmann, E., Ihlenfeld, H.-D., 1992. Life Strategies of Succulents in Deserts: With Special Reference to the Namib Desert. Cambridge University Press, Cambridge.

Edited by CH Bornman